History-dependent variability in population dynamics during evidence accumulation in cortex

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Summary

A fundamental feature of neural processing is combining ongoing activity dynamics with stimuli from the outside world. The posterior parietal cortex (PPC) performs this combination for a variety of computations, including evidence accumulation during decision-making. However, due to previous technical limitations, it remains poorly understood how the combination of external stimuli and internal activity, and thus evidence accumulation, are represented in a population of neurons. Here we developed an evidence accumulation task for mice navigating in a virtual environment and used two-photon calcium imaging to measure the activity of populations of individual PPC neurons. The PPC population represented task-relevant features, including choice and accumulated evidence, as a code distributed across groups of neurons that for the most part had heterogeneous and variable activity patterns. Using population-level analyses based on clustering of trials with similar activity patterns, we found that population activity trajectories were highly variable across trials, even for trials with identical stimuli. This variability was not entirely due to noise; rather, it contained structure that predicted past and future activity patterns over seconds, as well as future behavioral outcomes. Information about past events, including the previous trial's choice and the sequence of past stimuli, was represented in the population activity and contributed to the trial-trial variability. Our results suggest that, in the PPC, incoming stimuli are incorporated into a distributed code that contains a signal for past events, such that variability in a stimulus's representation in part reflects an ongoing historical record. These dynamics could allow the readout of accumulated evidence for decision-making and, more generally, any combination of internal activity and incoming stimuli.

Additional detail

We believe this study is of significant interest for both scientific and technical reasons. Technically, we developed an evidence accumulation task for head-restrained mice in virtual reality. In this task, mice are presented with six visual cues (spanning 5-6 seconds), presented one-by-one on either the left or right. Mice must decide if more cues were presented on the left or right in order to navigate to the appropriate maze location to receive a reward (Fig. 1). We performed two-photon calcium imaging from typically > 300 layer 2/3 PPC neurons during the task. To analyze the imaging data, we developed a novel, clustering-based approach to quantify how neuronal population activity changes over the course of single trials. Within each of ten epochs corresponding to different portions of the trial (e.g., cue 1 or early delay), we used affinity propagation, a message-passing based clustering algorithm, to cluster trials based on their neuronal population activity patterns. Each cluster is therefore a group of trials with similar activity patterns (Fig. 2a). Clustering identified population activity patterns relevant for key task features even though it was performed on neuronal activity and did not receive any information about behavioral parameters (Fig. 2b). This approach has proved an effective way to visualize how neuronal population activity patterns change over the course of single trials within a complete dataset.

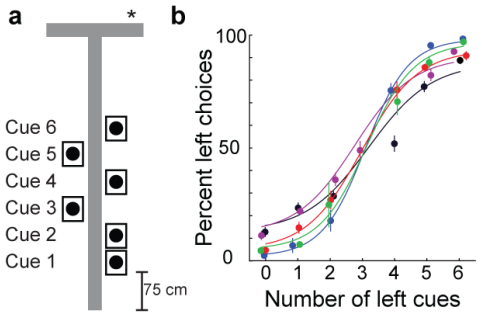

Figure 1 | a, Schematic of an example 2-4 right trial in a virtual T-maze. Asterisk marks the reward location. **b,** Performance for the 5 mice imaged (mean ± s.e.m, 7-12 sessions).

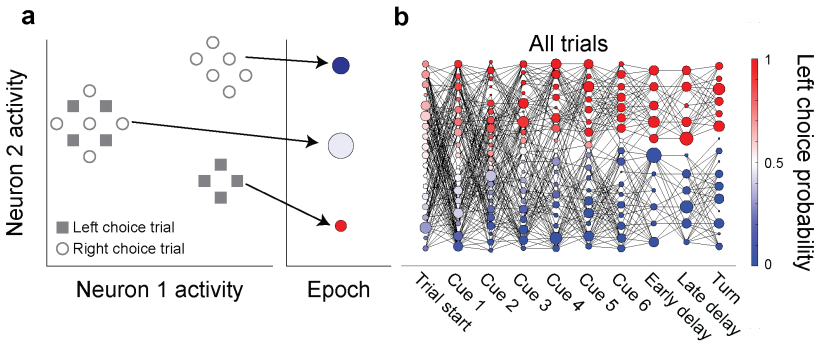

Figure 2 | a, Schematic demonstrating clustering procedure. **b,** An example transition matrix constructed from all trials in a single dataset. Nodes represent clusters with area proportional to the number of trials in the cluster, and edge widths between nodes represent the forward transition probability.

Scientifically, we found that while a small subset of neurons demonstrated selectivity for choice and accumulated evidence, the majority of neurons had activity that was mostly non-selective for task features and highly variable across trials. Population classifiers trained on these non-selective neurons, however, effectively decoded task features, suggesting that information in the PPC was distributed across populations of neurons. Using the clustering approach, we found that the current population activity pattern was predictive of activity patterns for at least 4-5 seconds into the past and future, even on trials with identical evidence cues and choices, indicating that variability across trials was structured across time. One source of this variability was the outcome of the previous trial, such that both the previous trial's choice and reward outcome (correct or incorrect) could be decoded well into the current trial, and in some cases, for more than 10 seconds following the conclusion of the previous trial. Different sequences of evidence cues resulted in distinct population activity patterns, even for the same accumulated evidence levels.

Together, our results suggest a generalizable feature of dynamics in the PPC in which stimuli cause distributed changes in activity that influence future population activity patterns and thus representations of future stimuli and choices. This feature was apparent as a history signal for past events (i.e. choices and cues) that caused predictive variability between single trials. Our results motivate a new model for evidence accumulation that is related to liquid state machine models and is consistent with previously considered low-dimensional attractor models. In this new model, each evidence cue is predicted to cause a distributed change in population activity that reverberates over time and combines with new cues, such that different sequences of cues result in unique activity patterns. The accumulation of evidence for different choices is predicted to occur in a winnerless manner, such that neuronal competition for the encoding of evidence for different choices is not necessary.